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BIOLOGICAL BULLETIN

ON THE LIGHT RECEPTIVE FUNCTION OF THE MARGINAL PAPILLÆ OF GONIONEMUS.[1]

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INTRODUCTORY.

On the oral or subumbrellar margin of the jellyfish *Gonionemus*[2] there are somewhat spherical or cordate papillæ, corresponding in number to the tentacles, and almost directly underneath the proximal ends of the tentacles. They are a bright translucent rust color with darker pigment lining the interior. The cavity is a continuation or pouch from the circular canal, thus insuring abundant nourishment for them. To distinguish them from marginal bodies, by which name Cœlenterate writers generally designate the otocysts, these organs are called marginal papillæ. Nutting[3] calls them sense bulbs, and Hargitt[4] and Goto[5] refer to them as "basal bulbs," Hargitt[4] describing them as "of brownish color delicately tinged with bright green." He also ascribes visual function to them.[6] The beautiful green spots

[1] To the management of the Marine Biological Laboratory I owe the material assistance enabling me to carry on my work and for this I am much indebted.

[2] The Woods Hole species is, of course, the one in question. Hargitt in "The Medusæ of the Woods Hole Region," p. 53, under the synopsis of *Gonionemus murbachii* Mayer, says: "This species was first described by A. Agassiz in 1862 from the Pacific coast. In 1895 a species was found at Woods Hole and supposedly identified with the Pacific species by Murbach, but it has since been classified as a distinct species by Mayer." This "supposition" is gratuitous. By using only the genus name in my report I meant to indicate my doubt about the identity of the species.

[3] Nutting, C. C. ('01), "The Hydroids of the Woods Hole Region," U. S. Fish Commission Bulletin, 1899 (Publ. 1901).

[4] Hargitt, Charles W. ('04), "The Medusæ of the Woods Hole Region," Bulletin of the Bureau of Fisheries, Vol. XXIV., 1904.

[5] Goto, Seitaro ('03), "The Craspedote Medusa *Olindias* and Some of its Natural Allies," The Mark Anniversary Volume, Art. I., pp. 1–22, 1903.

[6] *Loc. cit.*, introduction.

are in the bases of the tentacles, due apparently to refraction and reflection from brown pigment granules in the free ends of the endoderm cells of the tentacle insertion. As I understand that "basal bulbs" refers to the enlarged proximal ends of tentacles, or bulbs into which the tentacles are inserted, I do not use this expression.

To these marginal papillæ, under the name of marginal bodies, Yerkes [1] ascribes a special light-recipient function; he says, "the probability is strong that they are the special organs of photic stimulation." This conclusion seems to be based on the location and heavy pigmentation of the papillæ, and also on some experiments which will be referred to farther on.

In the Challenger Report on the Deep Sea Medusæ (Vol. IV., p. lii), Haeckel said: "As experiment showed, it is principally the swollen bases of the tentacles which bear such pigment eyes, and that chiefly in the order of the Anthomedusæ and in those Leptomedusæ which have no marginal vesicles. Such ocelli are more rarely found in Trachomedusæ, Narcomedusæ, and Stauromedusæ." Again he says: "Moreover medusæ perfectly devoid of color which have neither marginal ocelli nor other pigment spots, are sensible to light; in this case it is probably the sense epithelium of the umbrella margin which discharges this function."

Now wherever there are special structures in the bulbs above referred to by Haeckel there is perhaps, no doubt that they serve for receiving stimuli of some external kind. In the Leptomedusæ and Anthomedusæ there are true tentacular bulbs and the pigment spots in them may serve in the reception of light. On the other hand, in *Gonionemus*, a trachomedusa,[2] the marginal papillæ are not tentacle bulbs and have apparently no special structures for light reception, unless we consider the presence of

[1] Yerkes, Robert M., Ayer, James B., Jr. ('03), "A Study of the Reactions and Reaction Time of the Medusa, *Gonionema murbachii*, to Photic Stimuli," *American Jour. Physiology*, Vol. IX., No. 5, 1903.

[2] While there can be little doubt about some of the positive trachomedusan characters of the jellyfish, Dr. A. G. Mayer has suggested to me that in the light of Goto's careful work (*loc. cit.*) classing it as a leptomedusa renewed examination of the otocyst organs would seem desirable. As this subject merits more space than can here be given I will only say that I have prepared new sections and carefully examined a rather large series and am convinced that the otocyst organs are derived from the endoderm.

much pigment to answer this requirement. In regard to this point Beer[1] ('01) said: "Mit dar viel zu alt gewordenen Ansicht, dass Pigment der wesentlichste und ursprüglichste Bestandtheil eines jeden Sehorganes sei muss endgültig gebrochen werden." And in a considerable paper he makes good this statement.

In regard to the structure of the marginal papillæ it may be said that most Trachomedusæ and some Leptomedusæ possess a welt or ring of tissue made up of ectoderm, enlarged especially at, or near, the bases of tentacles by the rapid growth of cells for the production of nettling organs[2] which are to migrate out on the tentacles. In Goto's description of *Gonionemus depressum*[3] it is stated that "these bulbs . . . contain hollow prolongations of the entoderm of the circular canal, and the ectoderm is clogged with developing nettle cells." Perkins shows this structure in two figures.[4] The main point is that there is here no definite arrangement of either cells or pigment such as is present in so-called primitive eyes or eyespots. So that these papillæ would scarcely be expected to function as special organs for light stimulation. This does not preclude their being tactile; they are ciliated.

From experiments Yerkes finds[5] that when the oral surface is up, *Gonionemus* is much more sensitive to light than when the aboral surface of the animal is turned toward the light. This is supported by his observations that in a weak light the bell margin is turned upward and in strong light it is turned downward. The tentacles are cut off and, testing the animal, he finds that while the tentacles are sensitive to light they are not the cause of the difference in sensitiveness between the oral and aboral surfaces of the medusa. After removing the whole margin of the bell Yerkes finds that the remainder of the bell is not sensitive to light, or at least does not provoke response. Then

[1] Beer, Theodore ('01), "Ueber primitive Sehorgane," 1901.

[2] Murbach, L. ('94), "Beiträge zur Anatomie und Entwicklung der Nesselorgane d. Hydroiden," *Archiv für Naturgeschichte*, 1894.

[3] *Loc. cit.*

[4] Perkins, Henry F. ('02), "The Development of *Gonionema murbachii*," *Proceedings of the Acad. of Nat. Sciences of Philadelphia*, November, 1902 (March, 1903).

[5] *Loc. cit.*, page 300.

he adds (p. 302) that animals, whose tentacles were removed in such a way as to destroy the marginal bodies, never reacted to light; this, casually mentioned, as if it were not important. Yet this should be the crucial experiment.

Now since the marginal papillæ in *Gonionemus* are not true tentacle bulbs, and are only connected with the tentacles by the outer layer of ectoderm, and since the tentacles when pulled off by mérely seizing them always, in my experience, break off at their bases, leaving the latter, I could not see how the operation above referred to could be performed. It would be possible by seizing papilla and tentacle-base with forceps, but this would remove the margin of the bell with the nerve ring.

Problem.

These considerations led me to make experiments, first: to determine whether the light reactions of *Gonionemus* are dependent on stimulation of the marginal papillæ, or, second: whether any other set of organs, *e. g.*, the tentacles, the velum, or the gonads, also have this function.

Methods.

The first experiments were made by cutting the papillæ away from the margin with fine sharp scissors in such a way as to injure as little as possible the adjacent parts. Operated animals were left until they had recovered from the shock, or even for several days, but never long enough to allow the papillæ to regenerate. They were always compared with normal animals taken at the same time. Colors were also noted, as was the temperature of the water. In some of the experiments a 5 cm. deep saturated alum solution was interposed between the animals and the sun, but I have found with other experimenters, that this gives no advantage over plain water. The temperature varied no more than from one fourth to one and one half degrees centigrade in any of the experiments during an observation, and since the only purpose was to test the mere reaction of the papillæ or other organs, this change in temperature could be ignored. The medusæ were exposed in dishes of white glazed earthenware, in glass dishes, and in dishes with black substratum. It may

be remarked here that in the latter case the reactions were generally slower. The exposure was made in sunlight varying as it does during the middle portion of the day. For shutting out the sun absolutely opaque material was used; in some cases plain covers, in others covers that would completely darken the dish. While these give varying results in reaction time, they will not be considered here since constant conditions were maintained throughout any one experiment. In accurate time reaction experiments there should be some means of determining the exact intensity of light used. In some cases the exposure was uniformly for 60 seconds; in the earlier experiments only until reaction took place. The rest period I varied from 30 to 300 seconds; in general I found the former too short and the latter too long. Contraction leading to displacement was counted a reaction. From five to ten observations were made in succession and tabulated, but space will not here be taken for the tables in full. Only about one half the averages obtained will be given. It will be seen that I have followed somewhat generally the methods of Romanes,[1] Conant and Berger,[2] and Yerkes.[3]

Having received response to light in all cases where the marginal papillæ had been carefully removed, another cause of the reaction was looked for. Now as there is a thin welt of tissue connecting the papillæ which appears to be made up of similar cells, having about the same color, this welt of tissue might be conceived as taking over any light-percipient function that the removed papillæ were thought to possess; it was accordingly also removed. As this is a much more painstaking operation the work necessarily progressed slowly. In some cases a method was employed somewhat similar to the one previously adopted in removing the otocyst organs in the same medusa.[4] In other cases I depended on cutting away as little of the margin as possible and yet removing the welt of tissue in question, together with the papillæ. Such operated medusæ were usually tried in

[1] Romanes, G. J. ('76), "Jelly-fish, Star-fish and Sea-urchin," International Sc. Series, 1885.

[2] Berger, E. W., *Mem. Biol. Lab. Johns Hop. Univ.*, Vol. IV., 4.

[3] *Loc. cit.*

[4] Murbach, L. ('03), "The Static Function in *Gonionemus*," *Am. Jour. Physiol.*, Vol. X., No. 4, December, 1903.

from one or two to three days after the tissues in question were removed.

Results.

In all cases where papillæ were removed reactions still continued. As soon as such animals as had also the nettle welt removed were tested, the experiments were seen to be confirmatory of those on the papillæ. There was always a definite response to light stimulus, but in some cases it was slow. And it is still noticeable that the oral side of the medusa was more sensitive to light than the aboral. It ought to be stated here that the velum was always removed with the welt of tissue and it was not necessary to wait for its regeneration in order to get responses to light.

To determine if any of the other marginal organs or even any of the organs on the oral side of the animal had anything to do with the light perception, exclusively, or whether, as I began to think, it was the function of more than one organ — perhaps the subumbrellar epithelium in general — other organs which it was thought might be stimulated by light were removed. The ovaries, the velum, and the tentacles were in turn cut away. It is difficult to remove the velum entirely, as the closest cutting that can be done with the finest scissors leaves a narrow bit of the attachment of the velum on the margin. However, since the velum may be entirely removed while removing the welt and papillæ, a differential result will give approximately the value of the velum. Although these operations are more or less severe for the size of the organism, yet I have never observed so severe a shock from any of them as recorded by Yerkes, viz., that they have not again recovered. Indeed, I have almost always removed all the tentacles together and do not remember to have lost any individuals from this cause.

A preliminary experiment on a normal one, one without ovaries, one without tentacles, one without the welt and papillæ, resulted as follows; For the normal the average reaction time was $7\frac{1}{6}$ seconds; for the one without ovaries $10\frac{3}{8}$ seconds; for the one without tentacles $20\frac{5}{7}$ seconds; for the one without nettle welt and papillæ $12\frac{1}{5}$ seconds. In the light of later observations these results, except the last, seemed too long, as those without ten-

tacles or gonads displayed a remarkable activity, probably due to the removal of these organs.

In one of the first experiments a normal medusa was compared with two of the same lot in which the marginal nettle welt and papillæ were removed. The averages of ten trials were as follows: Average reaction time of the normal medusa $8\frac{3}{5}$ seconds; a 12 mm. olive-colored operated medusa $9\frac{1}{2}$ seconds; a 6 mm. yellow orange operated medusa 12 seconds. Next to this in reaction time were the medusæ with gonads removed. The average of four sets of experiments was $13\frac{1}{3}$ seconds. For the velum the average was higher, being $27\frac{2}{7}$ seconds; and for the tentacles still higher being 29 seconds. Another case, four hours after removal of the tentacles gave an average of four seconds.

Discussion.

Now, comparing these, account must be taken of the operations necessary for the experiments. The removal of the tentacles is the simplest of all and least likely to prejudice the action of other parts, therefore these results are the least doubtful. The careful removal of the gonads can have very little detrimental effect, as no principal part of the nervous system is involved. The removal of the marginal papillæ may include some of the underlying tissues, and more of this is included when the nettle welt is removed in addition. The same is true when the velum is completely removed. In the experiment for the value of the velum the attaching margin had to be left in order not to injure the nerve ring too seriously. In view of these facts negative results after any similar operation, such as Yerkes obtained for the removed papillæ, must be looked upon as needing confirmation in other ways, rather than being considered a proof of the function ascribed to the organs under consideration. In the specimens without the attachment of the velum, and those with the nettle welt and papillæ removed we must bear in mind that parts of the nervous system are more or less affected.

Conclusions.

From the earlier experiments of removing the papillæ alone it is evident that they are not exclusively the organs of light stim-

ulation. From the later experiments we may conclude that the welt of pigmented tissue running around the margin of the bell from papilla to papilla is not important, if at all sensitive to light. And furthermore that the ovaries, tentacle and velum have practically no more to do with this function than other organs. Injury to the nervous system may account for the slow reaction when the margins were removed for marginal welt of tissue and the velum. If now none of these organs that have been tested are solely affected by light, indeed only seem to slow the reaction in proportion to the injury, it seems to indicate that the epithelial tissue on the subumbrellar surface, in general, is the responsive organ.